

The Role of Shell Geometry as a Deterrent to Predation in Terebrid Gastropods

by

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Abstract. High-spired gastropod shells vary in their susceptibility to attack by durophagous (shell-destroying) predators. Slender terebrid gastropods with small apertures are damaged significantly less often than less slender species when exposed to calappid crabs. When damaged, slender terebrids are killed significantly less frequently than less slender species. The actual cause of slender terebrids' lesser vulnerability is uncertain, but small aperture size, a geometric correlate of shell geometry, may be responsible for the observed differences. High-spired shells are probably less likely than other shell shapes to be attacked successfully by other durophagous predators.

Frequencies of repair marks have been interpreted by some authors as an index of a shell's effectiveness in deterring potential predators. In experiments conducted for this study, nonlethal attacks were as common on robust terebrids as on slender forms, despite the fact that a higher proportion of attacks on robust forms were successful. Comparison of repair mark frequencies obtained from laboratory experiments to those observed in local populations showed slender terebrids bore fewer repair marks than robust forms, although the differences were not statistically significant. These observations suggest that repair marks are not an adequate index of a turritelliform shell's vulnerability to durophagous predators.

INTRODUCTION

PREDATION by durophagous (shell-destroying) predators is a major source of mortality among temperate and, especially, tropical marine mollusks (VERMEIJ, 1977a, b, 1978, 1982a, 1983). Durophagous predators employ two fundamentally different tactics in attacking gastropod prey. One tactic is crushing and the second is peeling, where the shell is pared away leaving the snail exposed. Crushing is believed to predominate on hard substrates while peeling is understood to be more common on soft substrata (VERMEIJ, 1978, 1982a, 1983; PALMER, 1979), although both modes of predation are found in both types of habitats.

Marine gastropods have evolved a variety of morphological features which serve to deter durophagous predators, including spines (PALMER, 1979), axial ribs (BERTNESS & CUNNINGHAM, 1981; VERMEIJ, 1982a), shortened spires (KITCHING *et al.*, 1966), thickened apertural lips (VERMEIJ, 1977a, 1978, 1982a), and apertures constricted by teeth or very narrow apertures (VERMEIJ, 1977a, 1978, 1979, 1982a; HUGHES & ELNER, 1979; BERTNESS & CUNNINGHAM, 1981). This paper will ex-

plore further one possible consideration: the role of shell geometry as a defense against durophagous predators. More specifically, this study will focus on the interaction between terebrid gastropods and a predatory decapod crustacean, *Calappa hepatica* (Linnaeus).

The Terebridae (Coniacea) are a family of common sand-dwelling marine neogastropods. They are limited to tropical and temperate regions and are abundant in shallow waters throughout the Indo-Pacific region. The family first appeared in the Late Cretaceous (TAYLOR *et al.*, 1980) and now includes approximately 150 extant species (BOSS, 1971). The interrelationships of terebrid genera are not well understood but the family is believed to be derived from the Conidae or an intermediate between the Conidae and Turridae, from which the Conidae were also derived (RUDMAN, 1969). The evolution and diversification of this family are both part of a general Cenozoic radiation of predatory marine neogastropods (TAYLOR *et al.*, 1980) and a part of the Mesozoic Marine Revolution (VERMEIJ, 1977a), wherein a variety of predation-resistant taxa replaced older, less resistant taxa that dominated the Paleozoic and early Mesozoic faunas.



Figure 1

Calappa hepatica. Note the well-developed master cheliped and the large tooth on the dactyl that is used for peeling snails. Specimen was collected at Motupore Island, Papua New Guinea; carapace length is 65 mm.

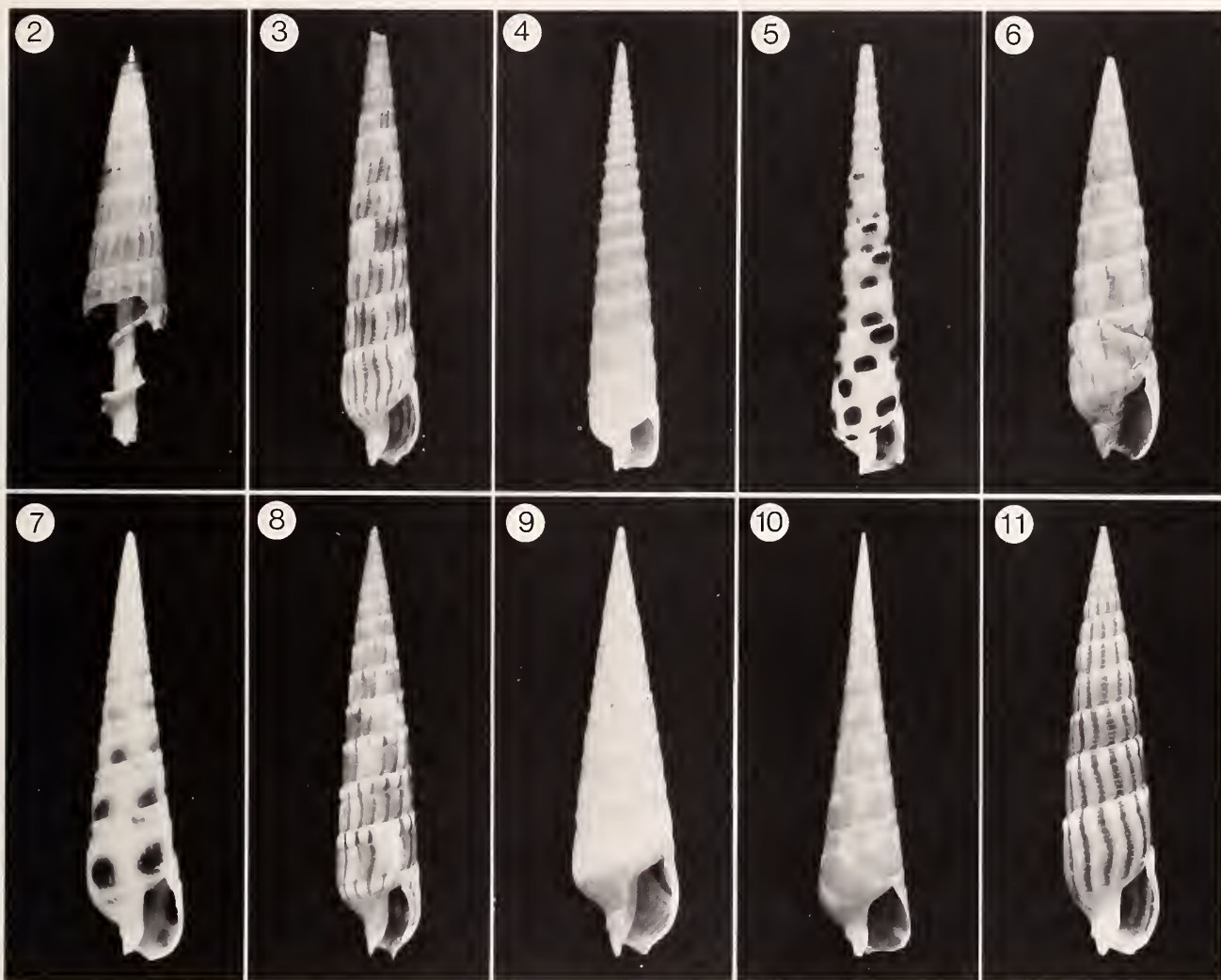
The natural history of terebrids is poorly known; only three species—*Hastula cinerea* (MARCUS & MARCUS, 1960), *Terebra gouldi* (MILLER, 1975), and *Hastula inconstans* (MILLER, 1979)—have been studied in any detail. Based on this limited information, it appears that durophagous predators, especially the sand crab *Calappa* (Figure 1) are important natural predators of small (<4 cm) terebrids.

Calappa is distributed throughout the tropical oceans of the world and commonly co-occurs with *Terebra*. It attacks its gastropod prey by peeling (Figure 2) (SHOUP, 1968; VERMEIJ, 1982a). The crab holds the prey with the small cheliped and uses its highly modified master cheliped (Figure 1) to peel away the shell. Unlike crabs from other families (e.g., *Cancer productus* RANDALL, *Eriphia sebana* [Shaw and Nodder] [ZIPSER & VERMEIJ, 1978]; *Ozius verreauxii* SAUSSURE [BERTNESS & CUNNINGHAM, 1981]), *Calappa* does not employ peeling as a mode of attack complementary to others, such as clipping the spire. Instead, *Calappa* is exclusively a peeler.

Morphological features that inhibit peeling, such as a

thickened outer lip or varices, have been shown to reduce the likelihood of a successful attack by *Calappa* (VERMEIJ, 1982a). Another possibility is that shell geometry or a correlate of shell geometry may confer resistance to peeling. A high-spined shell is actually a very long, thin, tightly coiled and slowly expanding calcium carbonate tube. A calappid crab would need to attack the shell through a small aperture and peel a high-spined shell further than what would be necessary for shells with a more trochiform geometry. Gastropods with very slender shells can often retract deeply into their shells, as much as several whorls into the shell (VERMEIJ *et al.*, 1980; VERMEIJ, 1982a). The small aperture of turritelliform snails may prevent *Calappa* from inserting its dactyl process to begin the peeling process.

VERMEIJ *et al.* (1980) tested the hypothesis that slender gastropods are more resistant to peeling. They predicted that if frequencies of attack were constant among terebrid gastropods, then those shells most resistant to predation should have a higher frequency of repair marks on their shells. Surprisingly, they found that slender terebrids ac-



Explanation of Figures 2 to 11

Figure 2. *Duplicaria baileyi* peeled by *Calappa hepatica*. The shell exterior has been peeled away leaving the columella intact. Shell length (to end of columella) is 15 mm.

Figure 3. *Terebra kilburni*. This and specimens in Figures 4–11 are from Motupore Island, Papua New Guinea. Shell length is 24 mm.

Figure 4. *Terebra laevigata*. Shell length is 26 mm.

Figure 5. *Terebra subulata*. Shell length is 28 mm.

Figure 6. *Terebra affinis*. Shell length is 22 mm.

Figure 7. *Terebra areolata*. Shell length is 23 mm.

Figure 8. *Terebra columellaris*. Shell length is 22 mm.

Figure 9. *Terebra conspersa*. Shell length is 21 mm.

Figure 10. *Terebra dimidiata*. Shell length is 47 mm.

Figure 11. *Terebra undulata*. Shell length is 23 mm.

usually had a lower average number of repair marks, implying that slender shells were more, not less, susceptible to peeling. This conclusion was supported in part by VERMEIJ (1982a), who found that a low frequency of repair marks implied that durophages were not present in the local habitat or that most attacks were successful.

The objective of this project was to provide a more direct test of the hypothesis that shell geometry or a correlate of shell geometry inhibits predation by peeling crabs. Also, the experiments allow comparison of actual success,

under experimental conditions, in avoiding predation by a durophagous decapod to repair frequencies in natural populations, thus permitting direct evaluation of the accuracy of repair frequencies as an estimate of a shell's effectiveness in providing protection against shell-destroying predators.

MATERIALS AND METHODS

Specimens of *Terebra* were collected from shallow (3–15 m) subtidal sand patches on the northwestern side of Mo-

Table 1

Results of offering slender and robust species of terebrids to crabs (*Calappa hepatica*). n is the total number of individuals of a given terebrid species offered to the crabs. Attacks is the number of those individuals damaged by the crabs. P_a is the proportion of individuals damaged by the crabs (attacks/n). Successes is the number of snails killed by the crabs. P_s is the proportion of successful attacks (successes/attacks).

	n	Attacks	P_a	Successes	P_s
Slender species:					
<i>Terebra kilburni</i>	55	4	0.08	0	0.00
<i>Terebra laevigata</i>	69	5	0.07	1	0.20
<i>Terebra subulata</i>	45	1	0.02	0	0.00
Subtotal	169	10	0.06	1	0.01
Robust species:					
<i>Terebra affinis</i>	22	3	0.14	1	0.33
<i>Terebra areolata</i>	15	1	0.07	1	1.00
<i>Terebra columellaris</i>	53	10	0.19	6	0.60
<i>Terebra conspersa</i>	53	10	0.19	7	0.70
<i>Terebra dimidiata</i>	12	3	0.25	1	0.33
<i>Terebra undulata</i>	46	10	0.22	5	0.50
Subtotal	201	37	0.18	21	0.57
Total	370	47	0.13	22	0.46

tupore Island (9°32'S, 147°16'E), in Bootless Bay, on the southern coast of Papua New Guinea. Individuals of over 20 species could easily be collected by sieving sand through a 3 mm mesh screen. The specimens were returned to the Motupore Island Research Center and maintained in a large water-table.

Sixty-eight percent of the snails were carefully examined under low-power magnification and the number of repair marks and shell length were recorded for each animal. Only well-defined repaired breaks that crosscut growth lines were counted. Only data for individuals ranging in size from 10 to 39 mm were used for this study (several of the species reach sizes in excess of 100 mm), in order to minimize the size bias in the numbers of repairs expected on any one snail (VERMEIJ *et al.*, 1980).

Calappa hepatica (Linnaeus, 1758) is abundant on sand flats at the north end of Motupore Island. The crabs are active at high tide and can be collected by hand as the tide recedes. Six crabs ranging from 41 to 65 mm in carapace width were collected and each was transferred to a running seawater aquarium. Enough coarse sand was provided to cover the bottom of the tank and allow the crab to burrow completely.

The terebrids were divided into two shape classes: slender and robust. Species were assigned to the slender class according to the criteria suggested by VERMEIJ *et al.* (1980); slender species are those with 18 or more whorls when the shell is 20 to 29 mm in length, 20 or more whorls when the shell is 30 to 49 mm in length, or more than 21 whorls when the shell length exceeds 50 mm (Figures 3–5). Robust shells are those with fewer whorls than required for assignment to the slender class at specified

lengths (Figures 6–11). The slender species offered to *Calappa* were *Terebra kilburni* (Burch, 1965), *T. laevigata* (Gray, 1834), *T. subulata* (Linnaeus, 1767), and the robust species were *T. affinis* (Gray, 1834), *T. areolata* (Link, 1807), *T. columellaris* (Hinds, 1844), *T. conspersa* (Hinds, 1844), *T. dimidiata* (Linnaeus, 1758), and *T. undulata* (Gray, 1834) (Figures 3–11).

Each crab was simultaneously offered four or five (two slender and two or three robust) terebrids as potential prey. Rejected prey were not re-offered to the same crab, but undamaged individuals were occasionally re-offered to another crab. The prey were presented in the morning and remained in the crab's tank for 24 h. Twenty-four hours was selected as the test period because it was a substantially longer time than VERMEIJ (1982a) found necessary for crab attacks but minimized disturbance within the tanks. At the end of each trial the snails were recovered and the results recorded for each individual. The snails were classified as either not damaged, damaged but not killed (shell broken but animal not harmed), or killed (shell broken and some portion of the snail eaten). Representatives of each shape class were offered each day, but only one individual of each species was placed in the tank at a time.

VERMEIJ (1977b) has emphasized that there is an important size component to the outcome of any encounter between gastropods and predatory crabs. When the gastropod reaches a relatively large size in comparison to the crab it tends to become invulnerable to the crab's attack. Vermeij referred to this as the critical size. MILLER (1975) observed this effect in his study of *Terebra gouldi*, noting that individuals larger than a few centimeters were no

longer preyed upon by *Calappa*. To avoid a possible size bias in this experiment all the snails offered to the crabs were small in size, generally less than 35 mm. There was no apparent increase in susceptibility for small shells in the data.

Calappa attacks on the terebrids occurred infrequently, sometimes raising concerns that individual crabs might not be healthy. If a particular crab failed to damage any shells for several consecutive days, a juvenile *Strombus gibberulus* Linnaeus was added to that crab's tank. Healthy crabs attack *S. gibberulus* quickly and relatively easily (VERMEIJ, 1982a), and the snail's demise was taken as evidence of the crab's good condition. During the course of experiments reported here, none of the crabs became unresponsive.

RESULTS

Terebrids, 201 robust and 169 slender, were offered to the crabs (Table 1). Thirty-seven of the robust terebrids were damaged when exposed to *Calappa* and, of that number, 21 were killed. Likewise, 10 of the slender terebrids were damaged but only a single individual was killed. These data can be employed to answer two separate questions; first, are robust terebrids more likely than slender ones to be damaged and, secondly, once damage occurs is there a greater likelihood that damage to a robust terebrid will be fatal?

More than 18% of the robust species were damaged while only 6% of the slender species had the aperture lip peeled. The frequencies of damage differ strongly from those expected if the two groups were equally likely to be attacked and damaged ($\chi^2 = 10.13$, $P < 0.002$). Slender terebrids are much less likely than robust species to be damaged when exposed to *Calappa*.

Fewer than half of the terebrids damaged by *Calappa* were killed. Among the robust species, 57% of the attacks were successful. In contrast, only one of the ten (10%) slender individuals that were attacked was killed. Again, the two frequencies differ significantly from those expected if the two shapes were equally likely to be killed during an attack ($P < 0.02$, Fisher's Exact Test [SOKAL & ROHLF, 1981]).

The sum result of these two effects is that slender terebrids are not very likely to be attacked successfully by *Calappa*. Indeed, only one individual of the 169 slender terebrids offered was killed for a frequency of kills well below 1%. This frequency is far lower than that of robust terebrids or of other gastropod species reported by VERMEIJ (1982a).

Slender terebrids collected for this project averaged 0.64 repairs per individual while robust species averaged 0.78 (Table 2). This difference was not significant (Mann-Whitney test), nor was there any significant difference between the two groups in the proportions of individuals lacking repairs altogether (chi-square test).

Table 2

Repair mark frequencies on terebrids from the Motupore Island Research Center. All data are for snails between 10 and 39 mm in length.

	n	Repairs	Frequency
Slender species:			
<i>Terebra kilburni</i>	36	29	0.80
<i>Terebra laevigata</i>	92	60	0.65
<i>Terebra subulata</i>	26	10	0.38
Subtotal	154	99	0.64
Robust species:			
<i>Terebra affinis</i>	12	16	1.33
<i>Terebra areolata</i>	9	3	0.33
<i>Terebra columellaris</i>	45	31	0.76
<i>Terebra conspersa</i>	21	23	1.10
<i>Terebra dimidiata</i>	4	0	0.00
<i>Terebra undulata</i>	24	14	0.58
Subtotal	115	87	0.78
Total	269	186	0.69

DISCUSSION

While a pattern of increased probabilities of lethal and nonlethal damage for robust terebrids is evident, the underlying mechanism remains unknown. The disparity in frequencies of attack among slender and robust terebrids cannot be interpreted unambiguously. The differences could arise from the way *Calappa* locates its prey, from prey selection by the predator once potential prey are detected, or from how the snails are attacked once found.

Calappa searches for prey by moving over the sediment and probing for buried prey with its chelipeds (SHOUP, 1968; MILLER, 1975; personal observations). Prey with a smaller profile might be less likely to be detected. Because terebrids burrow with the long axis of the shell subparallel to the sediment-water interface (anterior end down), slender terebrids, by definition, will have a consistently smaller profile (see Figures 3-11). Nevertheless, this effect is too small to account for the tremendous difference observed in frequencies of attack. The slender species have a cross-sectional area parallel to the shell axis at least 70% as great as the most robust species used in the experiment. This difference is not sufficient to account for the threefold difference in frequencies of attack, although it might have some effect on the overall results. Furthermore, X-radiographic studies of burrowing terebrids show slender terebrids burrow less deeply than robust forms, and should be more readily detected by the crabs (Signor, unpublished data). (For example, the anterior end of an 8-cm *Terebra dimidiata* will be 2.4 cm below the sediment surface, whereas the anterior end of a similar size *T. subulata* will be only 1.4 cm below the surface. In both cases, the apex will lie just below the sediment surface.)

Another hypothesis is that slender terebrids are somehow less desirable food items, and are not attacked if discovered. This seems unlikely, as many durophagous crabs, including *Calappa*, are surprisingly unselective when attacking potential prey items, and freely attack gastropods they have virtually no chance of killing (VERMEIJ, 1982a, b). *Carcinus maenas*, while selective in its attacks on mussels (ELNER & HUGHES, 1978), attacks all *Nucella lapillus* it encounters regardless of size (HUGHES & ELNER, 1979). Crabs have even attacked plastic models of long-extinct bivalves introduced into shallow marine habitats (LA-BARBERA, 1981). *Calappa* will eat the soft parts of slender terebrids when removed from the shell (personal observations), so there is no reason to suspect the crabs find slender terebrids inedible. However, the possibility of selective feeding behavior by *Calappa* should not be discounted as no data are presently available to demonstrate that prey selection does or does not occur.

Aperture size is a likely cause of slender terebrids' relative invulnerability to attack. Other researchers have observed that narrow or occluded apertures inhibit attack by predatory crabs (e.g., VERMEIJ, 1977a, 1978, 1982a; HUGHES & ELNER, 1979; BERTNESS & CUNNINGHAM, 1981). The results presented here are consistent with, but do not demand, that hypothesis.

Calappa possesses a large tooth on the dactyl of the master cheliped that meshes with two protuberances on the propodus (SHOUP, 1968). *Calappa* uses this tooth to peel away portions of the shell lip. The small apertures of terebrids, especially the more slender species, probably restrict the insertion of the calappid peeling tooth, in much the same way that a narrow or occluded aperture restricts access. Interestingly, the only slender terebrid killed was one attacked by the smallest calappid used in the experiment.

Regardless of the mechanism, slender terebrids are damaged or killed significantly less often when exposed to *Calappa*. This pattern seems to extend to comparisons between terebrids and forms with low spires. Overall, the frequencies of successful (fatal) attacks on *Terebra* by *Calappa* were far below those reported for other species by VERMEIJ (1982a). Only 10% of the robust terebrids offered to *Calappa* were attacked successfully, a result close to that observed by Vermeij for *Terebra affinis* (9.1%) and well below frequencies obtained for *Rhinoclavis aspera* (16%), *R. fasciata* (25%) and *Strombus gibberulus* (33%).

Terebra is also susceptible to shell crushing, the other mode of durophagous predation. Small rays are common in many of the shallow subtidal sand patches around Motupore Island and prey on mollusks and crustaceans dug out of the sediments with jets of water. But shell geometry might also serve to inhibit predation by shell crushers. Shell crushing fish must take the gastropod into their mouth in order to crush the snail with their jaws or pharyngeal mill. A long, slender shell could likely be more difficult than other geometries for the fish to manipulate

into the mouth for crushing. The effect of shell geometry as a defense against shell crushers has not been examined and would provide a useful complement to the results presented here.

VERMEIJ (1982a, b) has argued forcefully that repair marks on gastropods can be employed as an index of a shell's effectiveness as a deterrent to predation. The results presented above indicate that this generalization does not extend to high-spired snails. Robust terebrids sustained by far the higher frequency of successful attacks but also had a (not significantly) higher frequency of unsuccessful attacks (7.9% vs. 5.3% for slender species). Likewise, robust species have a higher frequency of repair marks than slender species in local populations, although the differences are less marked than in the experimental results. (The discrepancy might reflect the activity of other durophagous predators in the natural environment.) The shells of slender terebrids exposed to *Calappa* usually escape damage. This phenomenon may explain why VERMEIJ *et al.* (1980) were unable to use repair marks to substantiate their hypothesis that slender terebrids are less susceptible to peeling predators.

CONCLUSION

When exposed to the durophagous predator *Calappa*, slender, many whorled terebrids are damaged significantly less frequently than robust species. When *Calappa* attacks and damages a terebrid, the damage is fatal significantly less often in slender species. Robust species also suffer non-lethal damage as often as slender terebrids. These results support the hypothesis that shell geometry, or a correlate of shell geometry, can be an effective escape from predators. Repair marks are not a valid index of shell vulnerability in terebrid gastropods.

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